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## THE JURASSIC LAGOONS OF SOLNHOFEN

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THE aim of the true paleontologist is the elucidation of the history of the earth, and by the term earth history I do not mean merely the physical history, but also the biological history, so that the result will be a complete picture of the relations of land and sea, the inhabitants of both, the climate, and the steady progress of events—both organic and inorganic.

Such a picture is one of almost infinite complexity, as we at once realize when we endeavor to comprehend the mutual relations of a single flora and fauna to one another and to their physical environment in even a small area of the earth's surface at the present time. If it is almost impossible to arrive at correct results in dealing with a contemporaneous flora and fauna, how much more difficult is it to deal with the often fragmentary remains that represent a mere fraction of the life of five or ten million years ago.

Shall we then merely accumulate bricks and wait for the master builder of the future to build our temple? Already the bricks have accumulated in piles, mountain high, that threaten to bury us, and we sigh for the master builder that never comes. The older paleontologists, taking their cue from the scholasticism of medieval speculation, drew pictures of Carboniferous or Jurassic landscapes and seascapes with a facile hand, but they were mostly catastrophists, and their materials were largely subjective rather than objective, so that to-day their results are considered largely fanciful.

It is a most useful practise for the scientist to follow the example of mercantile concerns and to periodically take an inventory of stock on hand, make up a balance sheet and write off the discarded theories, hypotheses and misunderstood interpretations of facts with which his subject rapidly becomes cluttered. For some geological times or in some areas the record is so imperfect that the task is hopeless. For other times and in certain favorable regions we can gather the various threads derived from a study of the sediments, from the fossil animals and fossil plants, and weave these threads into a definite pattern.

Such a region, a region with one of the most remarkable known assemblages of life—from earth, air and sea—is that of the lithographic stone quarries of South Germany. There is scarcely a museum throughout the world that does not contain some specimens from the Solnhofen lithographic stone, and while the Solnhofen quarries are less rich in fossils than others in the immediate vicinity, as for example those of Eichstädt, little attention has usually been given to exact horizon or locality.

Johannes Walther has given us an exhaustive summary<sup>1</sup> and drawn a picture of the life and environment of the late Jurassic at the time the lithographic stone was being deposited which in many ways should serve as a model and an inspiration for similar attempts for other times and in other areas. This scholarly work leaves little to be desired in the way of facts. The interpretations of these facts, however, made before we knew very much about the origin of such fine-grained calcareous muds as formed the commercial lithographic stone, are not always the only or the most likely deductions permissible.

Let us first of all glance at a few of the main features of Jurassic geography before describing Solnhofen and the relics of bygone life that are found there. What we now know as the Jurassic period of earth history was called the Oolite by William Smith, the father of stratigraphic geology, because of the frequent occurrence in the rocks of this age of oolitic limestones or limestones made up of tiny calcareous concretions that resembled fish roe. These were famous building stones, so renowned even that the monuments that marked the Mason and Dixon line between the dominions of William Penn and those of Lord Baltimore were of this material imported from the quarries at Portland on the south (Dorset) coast of England.

Alexander Brongniart, in 1829, proposed as a substitute for Smith's name Oolitic, the term Jurassic because of the extensive development of the rocks of this age in the Jura Mountains. Smith had divided his Oolitic series into many subordinate zones based upon their characteristic lithology and fossils, and these he grouped into three major divisions. The lower was called the Lias, the middle Dogger and the upper Malm—these all being local quarrymen's names in England that are still largely used in geological literature. They correspond to what Leopold von Buch, another grand old man of geology, in 1839 called the black, brown and white Jurassic. The Solnhofen

<sup>1</sup> "Die Fauna der Solnhofener Plattenkalke," *Bionomisch betrachtet*, Jena, 1904.

deposits fall in the third or youngest of these subdivisions—the Malm or white Jurassic.

During the long ages of the Triassic period the Paleozoic highlands of Europe had been very largely worn away by the slow processes of erosion, and the Jurassic history is in the main one of shallow seas gradually expanding over a land surface of low relief, and culminating in the almost complete flooding of the continent. North America, on the contrary, presents a striking contrast to Europe, for it is only in the Pacific coast region, and in Alaska, Texas and Mexico, that any marine Jurassic sediments have been discovered.

The Jurassic seas of Europe were prevailingly shallow and warm. They swarmed with life of all kinds, and their sediments were predominantly calcareous. The history of these successively expanding and contracting Jurassic seas, and of the teeming life of their waters, is a long and an intricate story—too long to be attempted in the present limited space. Possibly if it had not been for the regular succession of the strata and the abundance of beautifully preserved fossils in the Jurassic rocks of England, France and Germany, we should still be ignorant of the bearing of fossils upon stratigraphic succession and correlation. Certainly the rocks of no other age show so clearly the interrelations and replacements of what are usually called faunal facies, as do those of Jurassic time as they are traced from place to place.

The Solnhofen deposits came at a time just subsequent to the maximum extension of Jurassic seas which had occurred in the immediately preceding times, the rocks of which now constitute the Oxfordian and Kimeridgian stages. That the seas still covered a goodly portion of Europe is shown by the accompanying sketch map. This stage of the upper Jurassic is known as the Portlandian (from Portland, England) or Bononian (from Bononia, the old name for Boulogne, France).

Such a map, while based upon the synthesis of a vast number of observations, is necessarily conjectural in areas where rocks of this age are absent or unknown, and it then has to be determined if they had once been present and were subsequently eroded, or whether this particular area was above the sea at that time. Moreover, errors in the correlation of distant strata are fruitful sources of misconception, and, finally, since even the map for a single stage covers some tens of thousands if not hundreds of thousands of years during which the coast lines were gradually changing, it is obvious that such a map can only approximate the true geography of any time and might aptly be

compared with the awkward-looking snapshot of a running animal as contrasted with a motion-picture film of the same animal.

Turning now to the accompanying map, it will be noted that Europe was an archipelago at that time, not unlike the East Indies of to-day. The largest island, probably of a much more irregular outline than I have indicated, embraced Scandinavia, Finland and northwestern Russia. No traces of Portlandian sediments have been found in this vast region except in the lined area indicated around its margin. A shallow open sea appears to have covered most of Russia, broken by large islands in the Caucasus, and in Podolia, Kiev, Bessarabia, Kherson and Taurida, that is to say, southwestern Russia and the Roumanian border. Asia Minor was above the sea, and it is uncertain whether this last land mass extended to the northwest, or whether parts of Macedonia, Bulgaria, Serbia and Hungary constituted another large island. Ireland, Scotland and western England were above the sea, as was most of Spain and the site of the Pyrenees. There were smaller islands in the Alpine region and elsewhere in Italy, and a large island occupied the western Mediterranean, the latter sea reaching the Atlantic across southern Spain on the north and Morocco on the south.

The ancient rock-masses of Brittany and the Auvergne in France were land and it is uncertain whether or not the two were united across the Loire valley or whether the Atlantic fauna reached the Paris Basin across this area shown by broken lines on the map. Another large island extended from Norfolk across Flanders into Germany, and here also the map indicates by broken lines the uncertainty as to whether or not this island was connected with or separated from the island or islands on the site of Swabia, Franconia and northern Bavaria. The presence of traces of the Atlantic fauna in Germany has suggested that this fauna migrated in the northeasterly direction indicated by the arrow.

Along the southern border of this Swabian, Franconian, Bavarian island or islands, there were reefs, extending southward into France, which prevented the mingling of the Mediterranean fauna of the Danube Basin and Dauphiné with the Atlantic fauna of the Paris Basin. There were other extensive reef areas in the Alpine region, in Provence, and elsewhere at this time.

The horizontally lined areas on the map, Fig. 1, mark the range of the Atlantic or occidental fauna characterized by the ammonite genus *Pachyceras*. The NW.-SE. or diagonally lined

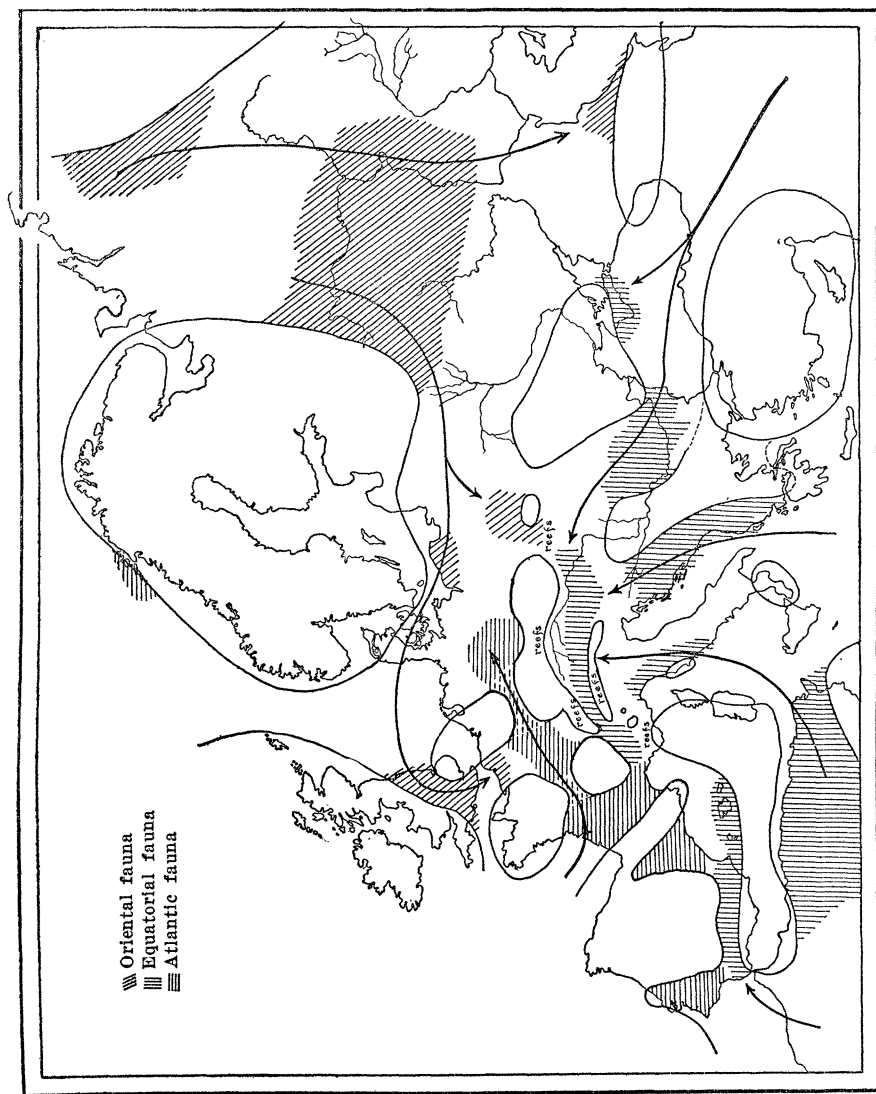


FIG. 1. MAP OF EUROPE SHOWING THE GEOGRAPHY AND FAUNAL FACIES OF THE PORTLANDIAN. (Modified from DeLapparent and Haug.)

areas mark what is known as the Volgian<sup>2</sup> or oriental fauna with numerous species of *Virgatites* and other ammonites along with *Aucella*, *Rhynchonella*, *Belemnites*, *Exogyra*, *Cylindroteuthis*, etc., which probably migrated as I have indicated by arrows. This fauna was formerly (*e. g.*, by Naumayr) thought to be an Arctic or boreal fauna, but this view has now been rather generally and quite rightly abandoned. The vertically

<sup>2</sup> Named by Nikitin in 1881 from its development in the Volga Basin.

lined areas show the range of the equatorial or Tithonian<sup>3</sup> fauna characterized by the ammonite genera *Oppelia*, *Perisphinctes*, *Phylloceras*, *Lissoceras*; by *Collyrites*, *Berriasella*, *Waagenia* and *Aspidoceras*, and by the curious brachiopods of the genus *Pygope* (*Pygope janitor* and *diphya*).

The lithographic stone comes principally from quarries on the hills bordering the valley of the Altmühl, a small northern tributary of the Danube, which it joins at Kelheim. They extend from Pappenheim to Pfalzpaint, a distance of between 15 and 20 kilometers, and are about 65 kilometers south of Nürnberg and about 85 kilometers slightly west of north of Munich. The lithographic stone is found as lenticular masses with a maximum thickness of about 75 feet in what seem to be depressions or basins in a heavily bedded dolomite or magnesian limestone known as the Franconia dolomite. The latter is rich in corals and other reef-building forms. The graphic section from Pappenheim to Eichstädt shown in Fig. 2 brings out this rela-

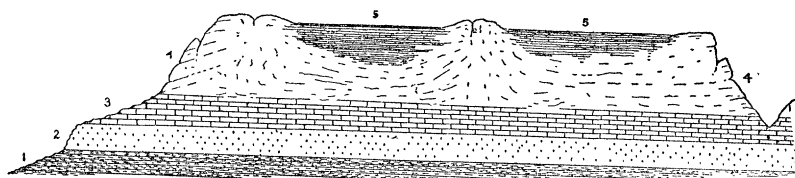


FIG. 2. DIAGRAMMATIC SECTION OF THE JURASSIC FROM PAPPENHEIM TO EICHSTÄDT.  
(After Walther.)

- No. 1. *Aulacothyris impressa* marl
- 2. *Peltoceras bimammatus* beds
- 3. Kimeridgian sponge limestone
- 4. Franconia dolomite
- 5. Solnhofen lithographic stone

tionship and exposes several of the older and underlying beds.

No. 1 is called the *impressa* marls from the abundance of the brachiopod *Aulacothyris impressa* (Bronn) and is of Argovian age.

No. 2 is called the *bimammatus* beds from the abundance in it of the ammonite *Peltoceras bimammatus* and is of upper Oxfordian or Rauracian age.

No. 3 is a limestone, rich in sponges, known locally as the schwammkalk and is of Kimeridgian age.

No. 4 is the Franconia dolomite and is of lower Portlandian age.

No. 5 is the lithographic stone, or Solnhofener Plattenkalk, as it is called locally.

<sup>3</sup> Named by Oppel in 1865 from Tithon or Tithonius, the husband of Eos, the dawn, from its fauna which is pre-nuncial to that of the Cretaceous.

The actual relations, as seen in the field, are not as diagrammatic as might be inferred from the figure. Conditions of sedimentation varied greatly from place to place, some layers yielding the commercial lithographic stone, others merely building stone. The sequence of beds in an individual outcrop may be illustrated by the following section at Mörsnheim quarry, copied from Gümbel's "Geology of Bavaria" (1894, p. 816) :

1. Soil and sandy beds with ammonites.....	3 meters
2. So-called fäule, rotten thin-bedded marly limestone.....	2 meters
3. Thick limestone bank with flints and ammonites.....	4 meters
4. Breccia-like beds rich in hornstone.....	1 meter
5. Silicious calcareous shales rich in <i>Terebratula</i> , <i>Rhynchonella</i> , <i>Terebratella</i> , etc. ....	5 meters
6. Rather massive siliceous limestone.....	5 meters
7. So-called ironstone with 260 thin and 25 thicker lithographic stone layers .....	20 meters
8. The so-called fäule, rotten marly limestone.....	10 meters
9. Irregularly bedded limestone, the so-called bottom stone....	5 meters
10. Franconia dolomite.	Total about 182 feet

Around Kelheim, where the Altmühl joins the Danube, the lithographic stone is replaced by a clayey coralline limestone which is known as the Dicerias limestone because of the abundance of these heavy-shelled bivalves. These are found associated with a few ammonites (forms characteristic of the north-west German and French lower Portlandian and including *Olcostephanus portlandicus* and *O. gravesianus*), but many corals, echinoids, Nerineas, fishes, turtles, crocodiles, pterodactyls, etc. Coral sand is present and the cross-bedding of the sands and the shallow-water heavy shells indicate a considerable surf.

Postponing to a subsequent paragraph the description of some of the wonders preserved in the lithographic stone, such as the earliest known bird, the numerous flying lizards and the dinosaur fetus, it may be noted that the fossils collected comprise an unusual assemblage, and undoubtedly denote special conditions of sedimentation. Thus molluscs are comparatively rare; bottom dwellers are practically absent; open-sea pelagic forms are mixed with a host of lobster-like crustaceans; jelly fishes left the moulds of their radiating gastric cavities in the muddy ooze; while a variety of tracks, insects and terrestrial forms add to the confusion.

Walther, after a careful analysis of the fauna, interprets the conditions as those of coral atolls with lagoons whose muddy bottoms were partly exposed and partly tidal. The calcareous



ooze as well as most of the life forms, already dead, he regards as having been swept into these lagoons by storms or unusual tides, while the interbedded clay-ironstone is considered to be wind-blown dust from the mainland which, following von Gumbel, he locates some 25 kilometers to the south of the site of the deposits in the region of the present Vindelican Alps.

It would seem to me that these Jurassic reefs were fringing reefs, or keys like those of southern Florida, rather than that they were comparable to atolls. That the mainland was much nearer than 25 kilometers is indicated by the lack of strong flying powers in the fossil bird, of which two rather complete specimens as well as isolated feathers have been found. That these birds were not carried to their calcareous tombs by currents after their dead bodies had washed into the ocean, but that they habitually resorted to these mud flats for the variety of menu there offered, is indicated by certain tracks on the surface of the mud which appear to have been made by an immature bird before its primaries were fully grown.

If storms were responsible for the wealth of organic remains accumulated in such small compass, surely coral sand would be more in evidence, as it is at Kelheim, or erratic heads and fragments of the reef corals would be commoner in the muds. In the studies inaugurated by Drew<sup>4</sup> and continued by Vaughan and his associates for the Carnegie Institution it has been demonstrated that the calcareous muds of the Florida keys and the Bahamas are precipitates, due to the action of denitrifying bacteria that are normally present in warm sea water, and the presumption is very strong that most if not all muds of this sort, both recent and fossil, owe their existence to the activities of such bacteria.

This then would reasonably account for the calcareous ooze that made the lithographic stone.

That a part of these muds at Solnhofen were tidal is very probable, since otherwise it is difficult to account for the host of forms of the sea-drift that came to be buried in them, but there is no evidence of tidal scour or wave action, and the waters must have been quiet and for the most part very shallow. The Jurassic *Limulus* or horseshoe crab haunted these muddy bottoms just as his modern brother is found in similar situations along the present Florida coasts or in muddy coves in higher latitudes, and the water was quite enough to preserve the trails of some of these Jurassic horseshoe crabs as well as those of some of their associates.

<sup>4</sup> Publication No. 182, Carnegie Institution of Washington, 1914.

Millions of stalkless crinoids of the genus *Saccocomma* of at least three species swarmed in these shallow waters and ammonite shells have been found preserved in an upright and life-like position.<sup>5</sup> Since the water was shallow and the bottom flat, these submerged mud flats would necessarily be exposed twice a day over wide areas by tidal action, which operated in Jurassic times with the same seeming inexorable and invariable regularity that it does to-day. It is a familiar experience that animals stranded on such mudflats seem usually to have an oriental belief in "kismet" and are as passive as if already dead. This and the further fact that many animals that properly belong in the open sea or in deeper waters are found at Solnhofen, and which must have been floated into the lagoons in a dead condition, are more readily understood than Walther's elaborate explanation, especially when it is recalled that there were decades to spare for their accumulation. They would inevitably have been smashed and not preserved so perfectly if they had been swept over the reefs by storms.

Upwards of 500 different kinds of animals have been recorded from the lithographic stone, but this is somewhat swollen by the true German thoroughness that has given every problematical scrap a binomial Latin name. Despite this, the lists are imposingly long and marvellous in the variety of life that is represented. Insects to the number of over 100 kinds were blown upon the mud flats or perished in the waters; sometimes we have preserved in stone the traces of the struggles of some mired insect in its efforts to escape. There are no fresh-water forms of life. Fishes to the number of nearly 150 kinds, mainly ganoids, have been discovered in these rocks. The crustaceans, which number over 70 varieties, are mainly lobster-like forms. The ammonites number 19 species distributed among six genera, and there were large numbers of the Jurassic ancestors of our modern squids or cuttlefishes. These number 17 species distributed among 8 genera, and some of them were very common individually and undoubtedly lived in the lagoons. Very often more or less of their soft bodies as well as their vestigial shells and pens were preserved as, for example, in *Acanthoteuthis*, in which the ink bag and the ten arms with their double rows of hooks were fossilized. There were many sea worms, free-swimming crinoids (comatulids) and brittle stars, and even such perishable and aqueous objects as jelly fishes were preserved with great fidelity in the fine-grained

<sup>5</sup> Rothpletz, A., *Abh. k. Bayerischen Akad. Wiss.*, Vol. 24, pp. 311-337, 1910.

ooze, where they were stranded by the retreating tide. Bottom dwellers of the sea are mostly absent and are represented almost entirely by molluscs that were accidentally washed into the basins or voided by fishes. A single dinosaur, evidently bogged, has come to light. Several kinds of crocodiles have been found, all of the long slender-snouted gavial type, and there were several species of marine turtles. The vertebrate inhabitants of the air that occur in these deposits furnish the most weird elements in the landscape that I am endeavoring to picture.

By all odds the most spectacular find in the lithographic stone was the remains of the oldest known bird—the *Archæopteryx* or lizard-tailed bird. Its uniqueness may be indicated by the fact that it alone constitutes a subclass (Archæornithes), while all other known birds are grouped in a second subclass (Neornithes). A single feather found in 1860 was named by H. von Meyer and shortly afterward a fairly complete individual was found at Solnhofen in 1861 and acquired by the British Museum. The enormous price that was paid for this specimen stimulated the quarrymen to a sustained interest in fossils and in 1877 a second and better preserved specimen was discovered near Eichstädt and is now in the Berlin Museum. Owen, who monographed the British Museum specimen, called it *Archæopteryx macroura*; Dames, who monographed the Berlin Museum specimen, called it *Archæopteryx siemensi*, while the original feather described by von Meyer had already received the name of *Archæopteryx lithographica*, which therefore has priority.

The two individuals supplement one another and undoubtedly represent the same or closely related species. They constitute one of the few great landmarks in avian paleontology, since no other known form shows so many reptilian features.

*Archæopteryx* was about the size of a modern crow. The head was small and flat, with very large eyes, and without body feathers except on the back and nape. There was no beak and both jaws were armed with small sharp teeth set in grooves. The nostrils were well forward and the body was long and narrow. The vertebræ were bi-convex and about 50 in number, of which only 10 or 11 are regarded as cervical (the lowest number of cervicals in any modern bird is 13). Instead of the few caudal vertebræ of modern birds terminated by a pygostyle for the support of the digitately arranged tail feathers *Archæopteryx* had about 20 elongated tail vertebræ, each of which appears to have supported a pair of tail feathers or rectrices, whose arrangement may be said to have been pinnate as opposed

to the palmate arrangement of all other known birds. In the embryos of some existing birds the caudal feathers are the first to develop, the tail is relatively elongated and is said to show a pair of feather sacs for each vertebra. The hind legs were slender, wide apart and far back in position, but were otherwise much as in modern perching birds, except that the tibia and fibula were distinct, as in most reptiles. The wings were short and rounded, with three separate sharply clawed and functional fingers. The wings carried rather large flight feathers, of which six or seven pairs appear to have been primaries and ten secondaries, and there was at least one row of wing coverts. The three pelvic bones are perfectly distinct, as in most reptiles, and similarly the ribs lack the hook-like processes characteristic of modern birds.

The fine-grained mud has preserved the feathers of the tail and wings with remarkable fidelity and traces of an incipient ruff at the base of the neck and rather conspicuous quill-feathers on the legs. No traces of body or contour feathers have been discerned, so that it may be concluded that the body was naked or was covered with down or tiny feathers that were not resistant enough to be preserved.

There has been much speculation regarding the true nature and habits of *Archæopteryx* and several restorations have been attempted. That by Heilmann, while somewhat realistic, is entirely too heavily supplied with contour feathers, the tail is too massive, and the birds are depicted as tearing at a cycad cone, although they were undoubtedly carnivorous, as their teeth clearly indicate. From the position and slenderness of the legs Beddard supposed that *Archæopteryx* must have stood on all fours when on the ground, but this is in a measure negated by the distinctly perching feet. Others have held that the absence of observable openings for the admission of air into the bones proved that *Archæopteryx* could fly only feebly if at all, but even such good modern flyers as swallows have practically non-pneumatic bones, and, moreover, we know that *Archæopteryx* resorted to the mud flats in search of food and hence must have flown from the mainland where it habitually dwelt. Finally, the well-developed feathering of the wings settles the question of flight beyond reasonable doubt. The labor of sustained flight with such short rounded wings may, however, have been compensated for by gliding, for which the wings and the quilled legs and distichous tail were admirably constructed and which historically must have preceded true flight. In an interesting

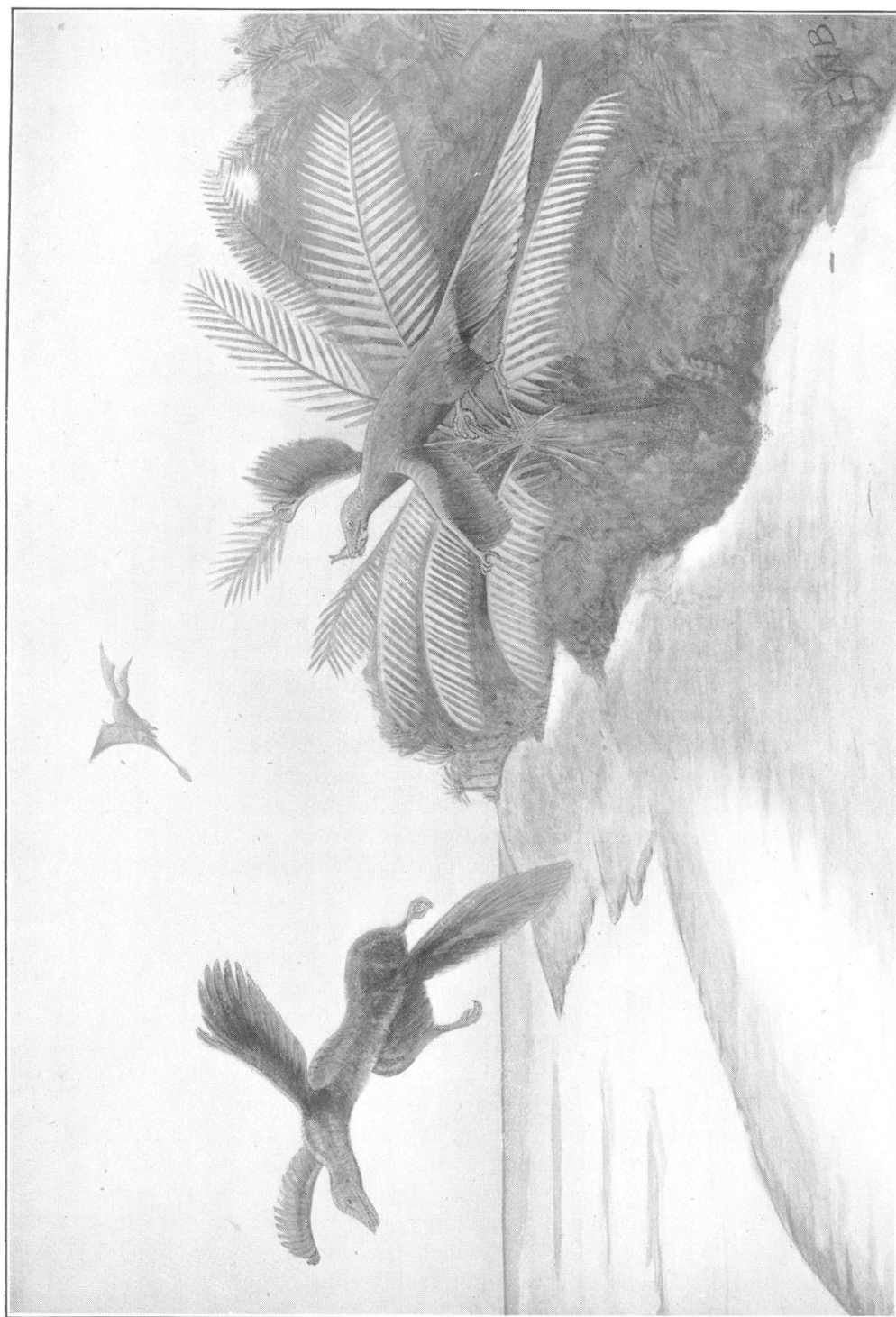


FIG. 3. RESTORATION OF THE EARLIEST KNOWN BIRD, *Archaeopteryx*

little article by Maurice Krosby,<sup>6</sup> from which I have copied the attitude, but not the details, of a flying *Archæopteryx*, it is implied that *Archæopteryx* had four wings; in fact, it is called *Tetrapteryx*, a name suggested by Beebe for the hypothetical ancestral bird.<sup>7</sup> Undoubtedly the quills on the legs made a plane of the hind legs, but they were not flapped, while the forelegs or true wings undoubtedly were flapped—the skeleton shows this much.

A comparison, rather remote, it is true, is suggested between the flight of *Archæopteryx* and that of the modern tinamous of South America, which have somewhat similar short rounded wings. As described by W. H. Hudson, the tinamous fly violently for a maximum distance of perhaps a mile, but usually a much less distance, and then glide to the ground, repeating this two or three times before becoming exhausted. The tinamous are ground dwellers and rapid runners, while *Archæopteryx* was, on the other hand, clearly a partially arboreal form and scarcely a runner. Its functional clawed fingers must have been habitually used in climbing about in the branches, much as a young hoactzin of South America does and they were also useful in effecting a safe landing in flying from one tree to another or at the end of a glide.

While *Archæopteryx* may be considered as about 25 per cent. reptilian, it is indubitably a true bird and a long way removed from its scale-covered and cold-blooded reptilian ancestors. There were bipedal bird-like reptiles already present before the close of the Triassic, so that there were some millions of years before the late Jurassic in which to evolve feathers and acquire the art of flying, and we know that the pterodactyls had successfully solved the problem of flight by another method in that same interval.

The present restoration (Fig. 3), which is believed to be far more accurate as to environment and detail than any heretofore attempted, shows the strand of the upper Jurassic mainland with the beach-ridges covered with a low jungle, made up largely of a mixed stand of cycads, with a few tall leathery fronded ferns, together with a scattering of taller conifers, comprising both scale-leaved (*Brachyphyllum*, *Palæocyparis*) and broad-leaved (*Araucaria*) types. High overhead is seen a small long-tailed pterodactyl or winged lizard (*Rhamphorhynchus*). In the foreground an *Archæopteryx* is flying. Note the slender body, the short heavily flapped wings, the pelvic plane made by

<sup>6</sup> *Popular Science Monthly*, Vol. 91, No. 1, 1917.

<sup>7</sup> *Zoologica*, Vol. 2, No. 2, pp. 39–52, 1915.

the widely spaced hind legs with their quill feathers, and the long distichously feathered tail constituting a second plane. At the right another *Archæopteryx* is shown with a small fish in its sharply toothed beakless jaws. It is perched on the crown of a *Zamites* of the *Williamsonia* order of cycadophytes. Note the long tail, the free clawed fingers of the fore limbs firmly grasping the cycad fronds and helping to sustain the long body.

Flying reptiles were evidently much more plentiful than birds during Solnhofen times, judging by the abundance and variety of their remains in these sediments, for nearly 30 different species have been described. They were weird bat-like creatures with pneumatic bones, large eyes, feeble hind limbs, and a keeled sternum for the attachment of the wing muscles like that of a modern flying bird. Their fifth finger had become enormously elongated and strengthened to support the membranous wings, which were thus exactly like the wings of a bat, with this exception, that only one instead of four fingers was elongated.

Ancestral pterodactyls go back at least as far as the Liassic or basal Jurassic. The Solnhofen forms were all relatively small and include over a score of species of the short-tailed *Pterodactylus* and five species of the long-tailed *Rhamphorhynchus*. Thus *Rhamphorhynchus phyllurus* had a total length of about 18 inches, of which two thirds was tail, and a wing spread of about 32 inches. An individual of the latter is shown, high in the air, in the accompanying restoration. Many thousands of years later, just before they became extinct, some of the pterodactyls lost their teeth and acquired bird-like bills and developed to gigantic size. Thus some of the pteranodons from the Upper Cretaceous Niobrara chalk of Kansas had a wing span of 18 feet, which is greater than that of any known bird.

Very many interesting tracks are preserved at Solnhofen, both those made on the emerged and on the submerged mud flats. These range from those of the Solnhofen *Limulus* or horse-shoe crab to that of an insect trying to extricate itself from the sticky mud, and include many that are problematical in character. One of the most well defined tracks that has been discovered and clearly that of some more or less bipedal vertebrate was early described and named *Ichnites lithographica* by Oppel. It consists of two rows of four-toed footprints at intervals of about 9 centimeters and about 7 centimeters between those of the right and left foot. Midway between the prints of the right and left foot is a small and shallow furrow of varying width and depth, apparently the trail of a dragging tail.

Alternating with the footprints and midway between them and the tail furrow are elliptical depressions with their long axes directed forward and outward. (This track is shown in Fig. 4.)

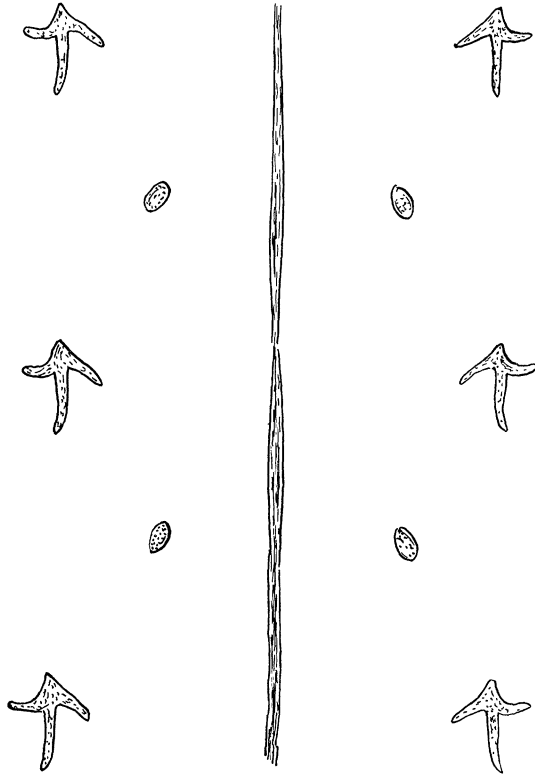


FIG. 4. PROBLEMATIC TRAIL, POSSIBLY OF AN IMMATURE *Archæopteryx*. (After Oppel.)

The question for decision is what sort of an animal made this track and how. Oppel thought that it was made by an *Archæopteryx* and many have followed him in this interpretation. Any small long-tailed animal with bird-like feet such as birds or some of the contemporaneous bird-like reptiles would readily account for the footprints and tail furrow, but how are the alternating elliptical tracks to be explained. They are too constant and regular not to have been made by the same animal that made the other parts of the trail. It has been commonly supposed that *Archæopteryx* made the whole trail by using its wings like a pair of crutches, the point of rest being the carpal or wrist joint. This is of course possible. Or it is possible that some other and as yet otherwise unknown animal made the tracks.



The chief objections to their having been made by a mature *Archæopteryx* are the small size of the footprints—much smaller than the feet of the two known specimens, the fact that the pinnately feathered tail would hardly leave a tail furrow in the mud that would look exactly like this one does, and that the wing quills would hardly permit of the wings being used as crutches. Nor is it easy to understand why the functional fore feet were not used. Moreover, if the weight rested on the wings, as assumed, the extremity would sink deep in the soft mud and hinder rather than help locomotion, as well as ruin the quills for purposes of flight. This would be equally true upon hard ground unless the quills were held in an unnatural way. It would further seem that if this were the true interpretation, the long slender body would demand that the ends of the wings rest farther apart. How the bird managed to hop at all, unless the wing-prints were one or more intervals in front of the corresponding footprints is difficult to understand. It is useless to deny the possibility of the accepted interpretation. I am, however, more inclined to think that while this trail belonged to *Archæopteryx*, it represents the trail of an immature and as yet practically flightless individual, which progressed in this way when on the ground—their small size might suggest this, and the difficulties about the wing and tail feathers would be obviated by their not having as yet become fully functional in size and possibly only sufficiently grown to permit gliding.

The terrestrial vegetation still remains to be considered briefly. Fossil plants have been known from Solnhofen since the days of Sternberg's "Flora der Vorwelt." In striking contrast to the variety and abundance of the animal remains, the traces of the former vegetation that clothed the near-by land are only occasionally met with in the lithographic stone, and even when present they are for the most part fragmentary.

The reasons for this absence of plants are to be found in the macerating action of the water, the non-deciduous character of the foliage of Jurassic plants, the activity of bacteria in the warm sea water, and most of all to the situation of the deposits, away from any estuary with its stream-borne load of land-derived débris. That these reasons are valid is corroborated by the fact that the few plants that have been discovered are such as have leathery decay-resisting parts such as cone scales and coniferous twigs, thus indicating that all the more delicate plant fragments had been destroyed, and by the additional fact that in other regions at this time where the sediments are more clearly of an estuary type as in the fish beds of

Cerin in France, a much more extensive flora as well as much disseminated vegetable matter and bitumen are present in the shales.<sup>8</sup>

The number of plant names in the literature would indicate that we knew a considerable flora from the lithographic stone, but a good many of these are names merely. Thus Saporta enumerated six coniferous species from Solnhofen, although at least half of these are now rightly regarded as synonyms of the remaining three. Similarly, Thistelton Dyer recorded 5 species of the coniferous genus *Athrotaxites*, although but one or two are valid.

Ignoring the doubtful impressions which have been described as seaweeds and which are without botanical value, there are at least four genera of Solnhofen ferns, so-called. The most abundant of these individually is *Lomatopteris jurensis* (Kurr) Schimper, and the others are forms of the genera *Sphenopteris*, *Odontopteris* and *Ungeria*, and some of them at least are not ferns, but relics of plants of the cycad or "sago-palm" alliance which frequently had fern-like fronds.

One of the most definitely identified plants is based on the characteristic one-seeded cone scales, which Dyer christened *Araucarites Häberleinii* and which unquestionably belong to the Eutacta section of the genus *Araucaria*, an antipodean group in the modern flora, but one that was world-wide in its Mesozoic distribution. Another satisfactorily determined conifer is *Brachyphyllum*, which has been entirely extinct since the Upper Cretaceous, but which was exceedingly ubiquitous throughout the Mesozoic. It had thick, club-shaped terete twigs with the leaves reduced to scales somewhat similar to those of a modern arbor vitæ or an incense cedar. Other twigs found at Solnhofen represent a cypress-like conifer variously called *Athrotaxites* or *Palæocyparis*; and *Ginkgo* and its extinct ally, *Baiera*, have also been identified, but with doubt, however.

The plants of these far-off Jurassic times are so different in every way from any that still survive that it is most difficult to picture their environment in terms of their physical requirements. We know that the climate was warm from the character of the calcareous ooze in which the fossils have been found. We presume that it was also humid from the kinds of contemporaneous terrestrial and arboreal animal life, and we also know that climates were more uniform then than now from the simple fact that the same Jurassic floras occur in the Arctic and Antarctic regions as are found in the equatorial zone.

<sup>8</sup> Saporta, G. de, *Ann. Soc. Agric. Lyon*, Vol. 5, pp. 87-142, pl. 14, 1873.

While it may be doubted if the reefs of Solnhofen supported a dense growth of vegetation, the mainland was more or less a jungle, although it was one prevailingly low in stature and one that might more appropriately be called a "scrub" or "bush." If we can imagine a chaparral made up of ferns and cycad-like plants with cypress-like conifers rising here and there above the general level, we shall have a fairly accurate picture of the Solnhofen woods. *Sequoia* cones have been found

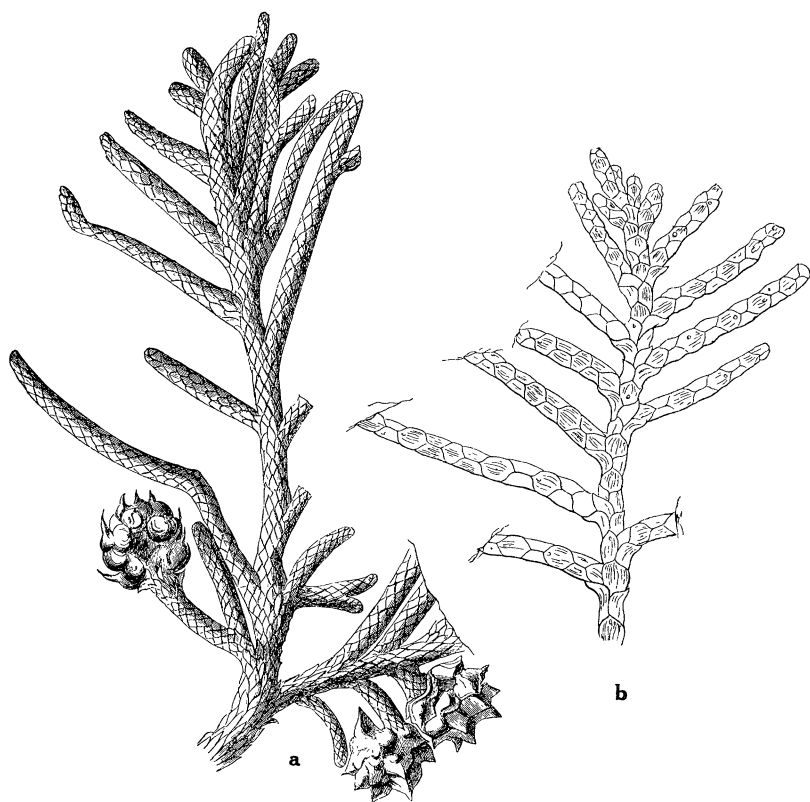


FIG. 5. TWO OF THE MOST COMMON CONIFERS FROM SOLNHOFEN. (After Saporta.)

a, *Brachyphyllum* (*Echinostrobus*) *Sternbergi* (Schimper)  
 b, *Palæocyparis* (*Athrotaxites*) *princeps* (Sternberg)

in the Portlandian of France, but all of the fossil sequoias were not giants like the California big trees. In Fig. 5 I have reproduced two of the commoner types of scale-leaved conifers that have been found in the lithographic stone, namely *Brachyphyllum* and *Palæocyparis*.